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THE STATUS OF THE MUTATION THEORY, WITH ESPECIAL REFERENCE TO ŒNOTHERA[1]

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THE more or less controversial literature of the mutation theory is so scattered and involved that few except specialists have been able to follow it with any degree of satisfaction. A recent book by Gates, "The Mutation Factor in Evolution, with Particular Reference to *Œnothera*," will help the general biologist to an understanding of the situation, but even in the short time since it went to press there have been developments of such significance that I am glad of this chance to review the subject.

The crux of the whole controversy is this: Are the discontinuous variations which occur in cultures of Œnothera true mutations, which might appear either in pure lines or in hybrids, or are they segregates from genetically impure lines? The mutationist and his Mendelian critic give diametrically opposite answers to this question. Some geneticists are beginning to feel that there is justification for taking a middle ground, that the mutations are non-Mendelian, but that they are nevertheless a phenomenon of hybridism, and occur only in impure lines.

The most extensive researches upon mutability have been carried out with *Œnothera Lamarckiana*. This

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plant gives rise to mutations of two main types, those in which the chromosome number differs from that of the parent form, and those in which it does not. The most striking ones belong to the former category; among them we need mention particularly only *Œ. gigas* and *Œ. lata,* which have, respectively, 28 and 15 chromosomes, instead of 14, the normal number in the species. Gates has especially emphasized the fact that in the mutating Œnotheras the pairing of the chromosomes, previous to the reduction division, is very loose, a condition that would favor irregularities in the distribution of the chromosomes to the gametes. By irregular reduction divisions, gametes with a greater or less number of chromosomes than 7 might easily be formed. From these irregular gametes there would be derived, in turn, zygotes with irregular chromosome numbers. Mutationists are now pretty well agreed that the characters of certain mutations are correlated with an unusual complement of chromosomes. If one believes at all that the chromosomes provide the mechanism of Mendelian inheritance, it is hard to escape the conclusion that the cytological studies of Lutz, Gates and others give a firm basis for removing at least part of the mutation phenomena from the domain of Mendelian segregation.

Even Davis, who has been one of the chief opponents of the mutation theory, has admitted that some of the variants from *Œnothera Lamarckiana* and other species are probably due to irregularities in chromosome distribution. He makes the point, to be sure, that the unpaired condition of the chromosomes previous to reduction in *Œ. Lamarckiana* is itself exceptional, and presumably the result of a hybrid constitution. Davis himself has shown that in at least one of the numerous strains of *Œ. grandiflora* which occur at the type locality of that species in Alabama, the chromosomes, in preparation for the reduction division, become associated definitely and closely into ring-shaped pairs. Moreover, this same strain shows a negligibly low pollen and seed sterility. Davis views it as essentially a genetically pure strain, whether judged by

its morphology or by its physiological behavior. In 1912 de Vries and the speaker visited the locality from which Davis's strains came, and found such a confusion of different types growing together that it was impossible to doubt that the entire Œnothera population was hybridized to a greater or less degree. Some of the forms belonged to the series of *Œ. grandiflora,* being large-flowered and open-pollinating, whereas others were small-flowered, self-pollinating types, showing obviously the effects of hybridization with *Œ. Tracyi,* another southern species. It is curious that the particular *Œnothera* to be put forward as probably genetically pure, judged by Davis's cytological criterion, or by Jeffrey's pollen test, should come from a locality where hybridization is so prevalent that one would hardly expect to find among the open-pollinating forms a single unhybridized plant. It will be remembered that Jeffrey has attacked the mutation theory from the point of view that pollen abortion necessarily indicates hybridity. By this criterion the small-flowered practically cleistogamous species which self-pollinate generation after generation must be adjudged highly impure, although the evidence is all to the contrary. There is every indication that pollen abortion is a frequent concomitant of mutation, as well as of hybridization. It seems not unlikely, therefore, that the unpaired condition of the meiotic chromosomes may have a causal relationship with pollen abortion as well as with the production of those types of mutations which have a chromosome number different from that of the parent species.

It is ordinarily supposed that a mutation is determined when the reduction division takes place. This may be the case with the mutations in which there are irregular chromosome numbers. Even in such cases it may be that the germ plasm has undergone at some other point in the life cycle a premutative modification of such a nature as really to predetermine the kinds of mutated gametes which will subsequently appear. A physiological premutation might, for instance, bring about the condition which results directly in loose chromosome pairing, and

indirectly in the formation of several different types of mutated gametes. Many mutations are not concerned with such obvious changes as the shifting of chromosomes, but seem rather to depend upon physico-chemical and chemical alterations of the germ plasm. Obviously some such alterations would result in physiological as well as morphological mutations. Just as certain morphological changes are not advantageous, or even distinctly harmful, so certain physiological changes might be harmful and lead to sterility. Some premutations (and by a premutation I mean the inauguration of an unstable condition in the germ plasm) might be of such a nature that the nutrition of the spore mother cells would be interfered with. These might fail to develop, fail to undergo the reduction division or might give rise to defective daughter cells.

Thus mutation, equally as well as hybridization, may account for sterility. There are several groups of plants in which sterility has apparently come about without the possibility of hybridization. Perhaps Davis's genetically pure *Œnothera grandiflora*, with perfect pollen, provides a case of hybridization without subsequent mutability. Those who assert that germinal instability comes about only by hybridization can bring forward no proof of their assertion. Conversely, the mutationist can not prove that any plant in existence has had an unmixed ancestry. The most that he can do at present is to show that mutation takes place in strains which are genetically pure, and that the purity is of relatively long standing. One can only conclude that Davis's and Jeffrey's suggested cytological and morphological evidences of hybridity, if verified, will merely substitute hybridization for premutation as a cause of germinal instability. They will not in any way afford support to the Mendelian conception of mutation.

Nothing could be more obvious than the paths which are marked out for the student of the *Œnothera* problem by the interesting cytological clue afforded by the unpaired chromosomes of *Œnothera Lamarckiana* and other

species. Some one must find out whether or not the unpaired condition occurs in hybrids whose parents do not show it. Strange as it may seem, after all the discussion of hybridity as a possible cause of mutability, no one has yet shown, or tried to show, that mutability occurs in any hybrid between non-mutable parent species. This would seem to be one of the most crucial experiments that could be performed, and one of the easiest. It would be a very attractive problem to attempt to produce the unpaired chromosome condition by hybridization and then to prove it definitely correlated with the particular types of mutability which are characterized by disturbances of the chromosome mechanism.

Even if it were possible in the time at my disposal to review the evidence that the chromosomes provide the mechanism of inheritance, it would hardly be necessary to do so. The brilliant work of Morgan and his students on the association in *Drosophila* of groups of characters with definite chromosomes is well known to every one. In *Œnothera* the investigations of Gates, Lutz and others have shown a connection between chromosome alterations and the characters of certain mutations so obvious that it can not reasonably be disregarded.

There are still a few geneticists, however, who believe that the chromosome cycle has no fundamental significance in connection with Mendelian phenomena. Heribert-Nilsson would ascribe as much weight to a change from flat to crinkled leaves, to choose an example at random, as he would to a change from the 2x to the 4x chromosome number. Such an attitude is forced upon one who attempts to explain all mutations as Mendelian segregates, as this author does. He has made much of a case, observed by Geerts and Stomps, in which the chromosome number of a hybrid between *Œnothera gigas* and *Œ. Lamarckiana* became reduced from 21 to 14, probably through the agency of an irregular reduction division, without the loss of the *gigas* characters. This case is cited to prove that the characters of this mutation do not depend upon the supernumerary chromosomes. Nothing

is more probable, however, than that the chromosomes are qualitatively different, and that the *gigas* characters depend upon the duplication of some, not all, of the chromosomes. An irregular reduction division might well result in the retention in duplicate of those particular chromosomes upon which the *gigas* characters depend. The very characteristic aspect of *Œnothera lata* has been ascribed to its single supernumerary chromosome. Miss Lutz has shown that many mutations with 15 chromosomes do not have at all the characteristic *lata* appearance, which must therefore be attributed to the duplication of a particular chromosome, rather than of any chromosome.

The production of mutations with irregular chromosome numbers is not confined to *Œnothera Lamarckiana*. Two other species have given rise to mutations with 28 *chromosomes*, and in one case, that of *Œ. stenomeres*, the *gigas* mutation is entirely comparable in its characters with *Œ. gigas* de Vries. Its wood structure has been compared with that of the parent species and has been found to present deviations as great as those which are apparent in the external aspects of the two plants. The differences concern not only the relative size of the elements, but also their shape, and, to a certain extent, their distribution. In typical *Œ. stenomeres* the medullary rays are sometimes 140 cells high, whereas in mutation *gigas* they are typically less than 25 cells high, and as far as we have observed, never over 50. It is very significant indeed that striking structural alterations in the most conservative tissues of a plant may be instituted by a single mutative evolutionary step.

As far as the mutations with modified chromosome numbers are concerned, there is the best of evidence that the processes of mutation and Mendelian segregation are absolutely distinct and independent. The evidence is not only cytological, but also genetical, for no mutations of this class show Mendelian inheritance when crossed with their parent forms. Their significance in evolution is illustrated by many widely separated groups of plants in

which species or genera are set apart from their allies by the possession of a different number of chromosomes. Such variations in chromosome number have been found in many cases among the Rosaceæ, a family noteworthy for the complications which it presents to the systematist. Certain Japanese species of Viola exhibit variations in chromosome number which give a clue to the way in which the numerous forms of this complex genus have evolved. Similar variations occur among the Orchidaceæ, one of the largest families of flowering plants.

There remain to be considered a large number of mutations in which the chromosome complement has not been shown to differ from that of the parent form. Such mutations are frequent in *Œnothera*. De Vries has observed them in the case of *Œ. Lamarckiana* and more recently he and other workers have observed them in other species, belonging to the small-flowered, self-pollinating portion of the genus. In connection with these mutations it will be necessary to consider more in detail the criticisms brought against the mutation theory by Bateson, Davis, Heribert-Nilsson and others.

In the past, most objections to the mutation theory have been based upon the supposition that *Œnothera Lamarckiana* is a hybrid of garden origin. I am forced to admit that I am not satisfied with any evidence thus far offered that this species, in the form familiar in cultivation, is or ever was a wild constituent of our flora. Nevertheless I venture to predict that it will eventually come to light in some obscure locality and that its character as a natural species will be established. Whether it is a natural species or a product of floriculture is of relatively little importance, however, in view of the fact that none of the mutation phenomena are peculiar to it. Several other species are known which are equally mutable and which are now elements of our flora. Moreover, they are small-flowered, self-pollinating forms, and therefore better suited to mutation studies than large-flowered, open-pollinating forms such as *Œ. Lamarckiana,* which in nature must frequently be hybridized.

Before mutation studies had been extended to other species of the genus from *Œ. Lamarckiana,* Davis began a series of experiments with the object of reproducing the latter species as a hybrid of known origin. His first experiments, involving *Œ. grandiflora* as one parent, were unsuccessful in producing a plant that bore more than a superficial resemblance to *Œ. Lamarckiana.* Some of the hybrids showed mutability, but none were obtained which did not show obvious segregation in addition to the mutability. Moreover, the mutations were not shown to have been induced by hybridization, since none of the parent strains were tested for constancy. As de Vries suggested, the mutability was probably an inherited tendency from one or both parents.

Later hybrids, between *Œ. franciscana* and *Œ. biennis,* were much more successful, in that they bore a much closer resemblance to *Œ. Lamarckiana.* The writer saw hybrids last summer in Davis's garden that would surely have been placed by any except the most ultra-critical systematist under *Œ. Lamarckiana.* They are being carried into another generation, and the results will be looked forward to with much interest. A true synthetic *Œ. Lamarckiana* must show mutability, but must otherwise come true from generation to generation. Moreover, it must give twin hybrids in certain crosses with other species. Even if Davis's later hybrids fulfill these conditions, they will not demonstrate the origin of mutability through hybridization, for one of the parents, *Œ. biennis,* has been shown by de Vries and Stomps to be a mutable species, and the other, *Œ. franciscana,* has not been tested. To have much weight, an experiment such as Davis's must show the origin of mutability *de novo* in a hybrid from non-mutable parents.

A more recent phase of the effort to prove *Œ. Lamarckiana* a hybrid dates from the publication, in 1914, of a paper by O. Renner. This author proposed a simple Mendelian hypothesis to account for the twin hybrids and high seed sterility of *Œ. Lamarckiana.* It is well known that in this species about half of the seeds are empty or

do not contain normal embryos. Moreover, when crossed with certain species, the first hybrid generation consists of two types, the twin hybrids of de Vries. Renner assumes that *Œ. Lamarckiana* is heterozygous and that it produces two types of functional gametes. Its progeny under ordinary circumstances would therefore be expected to consist of recessive homozygotes, heterozygotes, and dominant homozygotes in the familiar 1:2:1 ratio. He further assumes, however, that the homozygotes are incapable of developing beyond a young embryonic stage, and that the species is therefore maintained in a heterozygous condition from generation to generation. This simple hypothesis obviously does not account for the mutability of *Œ. Lamarckiana*. It has been amplified with this end in view by Heribert-Nilsson, whose highly involved explanation of mutability from the standpoint of the plural factor hypothesis must receive a brief consideration. For several years this worker has busied himself in an attempt to demonstrate Mendelian inheritance in *Œ. Lamarckiana*. In one case he thought he had found simple monohybrid segregation in crosses between red- and white-nerved races, and announced that the nerve color acted as a simple Mendelian character. It developed later, however, that his ratios were aberrant, and that the progenies entirely lacked a class of plants homozygous with regard to the supposed dominant character. According to Heribert-Nilsson's interpretation, the progenies consisted only of heterozygotes and recessive homozygotes. The elimination of the hypothetical dominant homozygotes he accounted for by assuming that in certain cases an incompatibility, or, as he puts it, a prohibition, exists between like gametes. His whole hypothesis is based upon this idea of prohibition. He assumes that the assemblage of characters which we recognize in *Œnothera Lamarckiana* may be brought about by many combinations of plural factors. Any one of these plural factors in the heterozygous condition gives a plant the *Lamarckiana* habit, and prohibition prevents the presence of any of them in the homozygous condition. Segre-

gation may lead to the production of pure recessives, lacking all the plural factors which give the *Lamarckiana* aspect. These recessives are the supposed mutations. Pure dominants, on the contrary, can not be realized.

This, in brief, is the Mendelian explanation of mutability. It involves the important assumption that the mutations which breed true are Mendelian recessives. The mutations with irregular chromosome numbers have been shown not to belong in this category. The remaining mutations, for many of which the cytological data are lacking, may conveniently be divided into two classes, (1) those which come true when self-pollinated, or, at any rate, do not include the parent species in their progeny, and (2) those which give a mixed progeny consisting of the mutational and parental forms. If there is any possibility whatever that the Mendelian explanation of mutability is true, it should at least account for the first and simplest of these two cases. We shall therefore confine our attention for the moment to mutations which give a constant progeny.

De Vries found that certain of the original mutations from *Œnothera Lamarckiana* were of the Mendelian type. These mutations are assumed by Heribert-Nilsson to be recessives which have corresponding homozygous dominants, the latter being the strains of *Œ. Lamarckiana* which do not give rise in every generation to the mutations in question. Other mutations, isolated by Heribert-Nilsson himself from *Œ. Lamarckiana*, are produced in every generation, and are therefore, according to this author, recessives which have no corresponding homozygous dominants. If this were the case, they would be recessive when crossed with *Œ. Lamarckiana* regardless of which way the cross was made. As a matter of fact, Heribert-Nilsson made his crosses with *Œnothera Lamarckiana* as the pistillate parent, and therefore obtained the results which he expected. If the crosses had been made the other way, there is very good reason to believe that he would have got the most unexpected results, and would never have advanced his Mendelian hypothesis.

The speaker has recently observed, in several species of *Œnothera* other than *Œ. Lamarckiana,* the origin of a large number of different mutations. Several of these have been found to belong to the type which we are at present considering. That is to say, they give a progeny which does not contain the parent species, and the mutations themselves are produced by the parent species in every generation. In the case of one mutation, described a year ago as *Œ. pratincola* mut. *nummularia,* the chromosome number has been determined as 14, the typical number in the group. The remarkable fact about these mutations of *Œ. pratincola,* as far as work with them has gone, is that their crosses with the parent species are identical with the pistillate parent in the first hybrid generation. Mutation pollinated with parent species yields the mutation. Species pollinated with mutation yields the species.

This most interesting state of affairs is absolutely at variance with the attempted Mendelian explanation. It can be understood on the supposition that two types of gametes are produced, which are by no means equivalent. One type bears most of the characters which differentiate the different species and forms from one another. The other type seems to carry characters which are likely to be common to a number of different species. In the particular species which gives rise to the mutations under discussion the gametes of the former class are female, those of the latter, male. Thus it follows that a mutative modification of the germ plasm in one of these species might affect only characters which were borne by one of the two kinds of gametes. If so, we would have at once a simple explanation of the behavior of the mutations which give matroclinic crosses with their parent species.

The same idea may readily be extended to cover the cases of mutations which give progenies containing both the mutational and the specific types. Perhaps the mutative change is a reversible one, and certain gametes in each generation show reversion from the mutated to the unmutated condition. Or perhaps in some species there

are male and female gametes of both types, but certain mutative changes are sex limited. In the following discussion I shall designate the two types of gametes as α and β gametes. The former are those which bear the most distinctive specific characters of the various forms, whereas the latter bear the more general characters. The known facts seem to be accounted for if we assume that in fertilization the conjugation of an α with a β gamete ordinarily takes place, but not the conjugation of two β gametes. In certain cases it seems that fertilization takes place by the fusion of two α gametes and it appears likely, also, that some species produce no β gametes. Some species produce α and β gametes of both sexes. Others do not seem to do so. It sometimes seems to be the case that the female gametes are all α. When a mutation takes place the modified character is perhaps Mendelian if it is borne by both α and β gametes, but non-Mendelian if it affects only the α gametes of a species in which fertilization takes place by the fusion of an α with a β gamete.

This conception of non-equivalent gametes has been highly developed by de Vries, in a somewhat different way from that outlined above. It has many obvious advantages in explaining the *Œnothera* situation. It explains seed sterility as well if not better than the Mendelian hypotheses of Renner and of Heribert-Nilsson, hypotheses which are based of course upon the idea of gametic equivalence. It explains why certain reciprocal crosses are alike, and others unlike, why some of them breed true, whereas others show segregation, why certain crosses yield twin hybrids, and why the twins are, respectively, matroclinic and patroclinic. It also explains other complications which are quite unintelligible from a Mendelian standpoint. I would by no means give the impression that there are not many phenomena which remain obscure, but I do wish to emphasize very strongly that a flood of light is thrown upon the *Œnothera* situation by the conception of non-equivalent gametes.

By way of illustration, let us consider for a few moments the phenomenon which I have called mass mutation.

Mass mutation differs from ordinary mutation only in that the mutations, instead of being produced in small numbers, are produced in very large numbers. For example, the frequency of mutations in *Œ. Lamarckiana*, which shows ordinary mutability, is roughly 2 per cent. In certain strains of *Œ. Reynoldsii* and *Œ. pratincola*, on the contrary, the number of mutations rises to 50 per cent., or even 100 per cent., of the progenies. According to Mendelian conceptions, it is impossible to get extracted recessives in a progeny in excess of 33⅓ per cent., and in order to get this many we must grant the elimination by prohibition of the corresponding dominants. What shall we say, then, of progenies containing 499 mutations out of 500 plants, a condition which has actually been realized in my cultures of *Œ. pratincola?* It is impossible to invoke the elimination of a large class of typical plants, for the typical zygotes are known to be stronger and better fitted to develop than the mutational zygotes. My own explanation is that most of the female germ cells of *Œ. pratincola* are α gametes and the male, β gametes. The phenomenon of mass mutation consists in the wholesale production of modified α gametes, α', α'', α''', α'''', etc., each of which corresponds to a different mutation and has characters which impress a distinctive habit on the zygote which is formed by fusion with an unmodified β gamete. In accord with this hypothesis the reciprocal crosses between mutation and parent species are matroclinic. Mutation pollinated with species gives mutation. Species pollinated with mutation gives species.

Mention has already been made of the mutations which by self-pollination give progenies containing both the mutational and the specific types. If the mutation is cross-pollinated with pollen from the specific type, the progeny is a mixture of two types, just the same as if self-pollination had occurred. On the contrary, if the specific type is pollinated by the mutation, only the specific type occurs in the progeny. Here, it seems, we have a case where the modification which results in the production of α' instead of α gametes is reversible. Cases of this kind

Heribert-Nilsson refers to (I give a literal translation) as "heterogamous combinations which are recessive only in the female gametes, but in the male gametes continuously heterozygous." As far as I can interpret this vague statement at all, it involves a decidedly unique conception, namely, that the individual $2x$ mutation embodies two different kinds of germ plasm, a homozygous female germ-plasm which will give one kind of cells when the reduction division takes place, and a heterozygous male germ-plasm, which will give two kinds of cells. I think that no one will be inclined to adopt this altogether revolutionary and useless hypothesis. It is by no means certain, after all, that the mutations which show the type of inheritance in question do not belong to the class with irregular chromosome numbers. With one exception they have not been examined cytologically. *Œnothera lata,* a mutation which shows this type of inheritance, has 15 chromosomes. Consequently there is an opportunity for the formation of two kinds of gametes, with 7 and 8 chromosomes, respectively. The male gametes with 8 chromosomes appear to be eliminated. As a result, zygotes are formed with $7 + 7 = 14$ and $8 + 7 = 15$ chromosomes. The former are *Œ. Lamarckiana,* the latter are *Œ. lata.* This beautiful correlation of cytology with inheritance has been worked out by Gates and Thomas.

In either event, whether the mutations which throw the specific type in every generation have a regular or an irregular chromosome number, the mutation hypothesis provides a far more plausible explanation for their behavior than the Mendelian hypothesis.

It must be clear by this time that the speaker finds incredible the arguments that have been brought forward in favor of the idea that mutation and Mendelian segregation are the same. Doubtless it often happens that a mutated germ cell fuses with a typical germ cell and produces an ordinary Mendelian heterozygote. If the mutated character is recessive, and the dominance is complete, the first hybrid generation will of course resemble the parental type, and the second hybrid generation will

show simple segregation. The mutation will appear for the first time in 25 per cent. of the progeny. De Vries has recently reported that the dwarf mutation from *Œnothera gigas* is of the simple recessive Mendelian type. We must believe, in a case of this kind, that the factor whose modification results in dwarfness is present in all gametes. It does not follow, however, that the gametes are all equivalent with respect to the factors for other characters.

In connection with the discussion of Davis's hybrids which resembled *Œnothera Lamarckiana* I mentioned that the mutability shown by them was probably inherited from one or both parents. There seems to be some scepticism about the inheritance of mutability as a character. Much of my own experimental work of the last two years has involved *Œ. pratincola,* a mutable species which has already been refered to several times. There is another species from the same locality which is rather closely allied to *Œ. pratincola,* but differs in enough regards so that the hybrids between them can be studied with great satisfaction. The second species, *Œ. numismatica,* is immutable, as far as my experience extends. At any rate it is very much less mutable than *Œ. pratincola.* The cross *Œ. pratincola* × *Œ. numismatica* gives twin hybrids, one of which is exactly like the pistillate parent except in one minor pubescence character. The reciprocal cross, *Œ. numismatica* × *Œ. pratincola,* is to all outward appearances the same as the pistillate parent. We have here a most striking case of matroclinic reciprocal hybrids. I am inclined to believe that most of the differences between the two species reside in the α gametes and that the β gametes are essentially similar. In accord with this hypothesis nothing could be more interesting than to find that the *pratincola*-like hybrid is mutable, and produces the same types of mutations that *Œ. pratincola* itself does. This result, it seems to me, is of the highest significance. It indicates that the germ plasm of *Œ. pratincola* is in a labile condition, and that this condition is not modified when a zygote is formed by the fusion of its α gamete with the β gamete of a different and stable, or at least relatively

stable, species. We could hardly find better proof that such mutations in *Œnothera* involve the α gametes, and are apparent in the zygotes without the need of subsequent segregation because the factors involved have no counterparts in the β gametes.

The same crosses, however, afford evidence that certain characters are carried by both α and β gametes, and may therefore prove to show Mendelian segregation. The buds of *Œ. numismatica* have a short viscid pubescence which is lacking in *Œ. pratincola*. The matroclinic hybrid *Œ. pratincola* × *Œ. numismatica* can be distinguished from the pistillate parent only by the presence of this hair-type, inherited from the pollen parent. When the second hybrid generation is grown, segregation with regard to this character takes place, and part of the progeny can not possibly be distinguished from *Œ. pratincola*.

In these results we have a clue to the segregation shown in certain hybrids, and the lack of it in others. Most of de Vries's hybrids have involved *Œ. Lamarckiana*, a species, according to my interpretation, with very dissimilar α and β gametes. He has therefore obtained and described many measurably constant hybrids. Davis, however, studying *Œ. grandiflora*, which may conceivably have but one type of gametes, has found segregation the rule rather than the exception. In his later studies, involving *Œ. franciscana* and *Œ. biennis*, he has obtained twin hybrids within each of which there was a considerable degree of segregation. All of these varying results will eventually become coordinated as we become more used to distinguishing between non-Mendelian and Mendelian characters.

Another point which must be mentioned is the frequence with which the various types of mutations give rise to one another. For example, two mutations of *Œ. pratincola*, mut. *nitida* and mut. *fallax*, each give rise to plants of mut. *numularia*, which are as typical as though they had been derived directly from *Œ. pratincola*. As already brought out, some mutations appear to be reversible in that they revert to the parent species in part

of every progeny. The germ plasm seems to be a system capable of existing in several different states of equilibrium. Some of these equilibria may be thought of as stable, others as metastable, others as labile, to borrow terms from the physicist. The germ plasm of different species may undergo parallel transformations, resulting in parallel variations. All who have dealt with the species of large genera know that oftentimes the same series of variations turns up in one collective species after another. Many characters have arisen independently, at so many points in different lines of descent, that they have no phylogenetic significance whatever.

It seems to the speaker that the *Œnothera* situation is clearing up. More and more evidence is accumulating which shows that although the phenomena are complex, they are orderly. Probably no two of the workers on the *Œnothera* problem look at it from the same point of view. In this paper I have not hesitated to state freely my present working hypotheses. Next year they may have changed, to fit new facts. Even now there are data at hand which do not accord with the best hypotheses I have been able to formulate, but neither do they accord with any others. Under the circumstances, one should not draw conclusions of too sweeping a nature. It may confidently be stated, however, that the appearance of mutations in *Œnothera* is not due to Mendelian segregation, and that the Mendelian method of attack has been utterly fruitless. It is freely admitted that the mutation processes themselves are hardly understood at all, and that further work must decide whether or not mutation is always or ever conditioned by previous hybridization.

Bateson has recently described the genetical behavior of the rogues which occur in certain varieties of peas. Although he does not suggest that these strange forms are mutations, his evidence would tend to convince a mutationist that they are. Would it not be a strange turn of fate if Bateson, the leader of the Mendelian school and critic of de Vries, were destined to discover mutations of a non-Mendelian type in the very genus which provided Mendel with the material for his classical researches?

INHERITANCE STUDIES IN PISUM

I. Inheritance of Cotyledon Color[1]

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Introduction

Modern students of genetics such as Baur, East, Morgan, Emerson, and others classify all variations in animals and plants into three general categories on the assumption that organisms are made up of unit factors, in the same way that a chemist thinks of rocks and minerals as being composed of elements. These three categories of variation are:

1. Variation resulting from changes in environment.
2. Variation due to "loss" or "gain" of new factors through crossing.
3. Variation due to mutation.

The Problem

The present paper has to do largely with data on variations in *Pisum* belonging to the first and second categories mentioned above. An attempt is being made definitely to work out the Mendelian or factorial constitution of the genus *Pisum* with reference to all those characters by which its few species and numerous varieties are distinguished. In order satisfactorily to accomplish this object, all or nearly all the known varieties of the genus *Pisum* must be considered. In this paper only the inheritance of cotyledon color is considered. Further papers

[1] Published as Brooklyn Botanic Garden Contributions, No. 10. These studies on the genetics of *Pisum* are being carried on in collaboration with the Office of Forage Crop Investigations and the Office of Horticultural and Pomological Investigations, U. S. Department of Agriculture. Based in part on a paper given at the Twentieth Anniversary Celebration, New York Botanical Garden, September 9, 1915.

will deal with other characters and the modifications of various characters through crossing.

Of more than two hundred and fifty varieties and species upon which the writer has been conducting experiments, the great majority have seeds which in the mature condition possess yellow cotyledons, but in such an array of varieties, it was soon noticed that the shades of yellow varied from a light greenish yellow to that of a deep orange. Roughly one could divide these forms with yellow cotyledons into light and deep yellows, but any one particularly "keen" on forming a series showing continuous variation, could easily grade the varieties so as to present a series without breaks from light greenish yellow to deep orange yellow. All the wild varieties and species so far examined have yellow cotyledons, which favors the assumption that yellow cotyledon is the oldest color character. Many of the cultivated varieties and especially the so-called blue "field peas" such as Wisconsin Blue and Prussian Blue and the majority of those known as "garden peas" have green cotyledons when the seed is mature. What has been stated regarding the gradations of color in yellow cotyledon varieties is equally true of those with green cotyledons. Roughly classified, there are dark and light green forms, but the various varieties can be arranged in a continuous series representing every shade from very dark green to light yellowish green.

Among the numerous green and yellow cotyledon varieties, when grown under the same environment, there are, however, many varieties to which certain distinct shades of either green or yellow are peculiar. Some varieties have characteristically deep orange cotyledons, others have light yellow cotyledons, and still others breed true to the shades between these two extremes. With the group of green cotyledon varieties, the same state of affairs holds true. Classification of yellows and greens is still further complicated because some varieties with light yellow cotyledons grade into the light greens and *vice versa*, even though both are grown under the same conditions.

The following table (Table I) gives the names of varieties of greens and yellows representing the classes dark

TABLE I

VARIETIES OF PISUM CLASSIFIED ACCORDING TO SHADES OF COTYLEDON COLOR WHEN GROWN UNDER THE SAME CONDITIONS

Yellow Cotyledons

Cotyledon Shade	Variety	Pedigree Stock No.	Source
Orange yellow	Black-Eyed Marrowfat	14	Vaughan Seed Co.
	First of All	22	P. Henderson & Co.
	Petit Pois	25	P. Henderson & Co.
	Späte Gold	29	Haage & Schmidt
	Henderson's Perfection Sugar	60	P. Henderson & Co.
	Agnes	147	S.P.I. 22036
	Admiral	159	S.P.I. 29323
	Khaba	176	S.P.I. 20380
Yellow	Mummy	1	H. Eckford, Wem, Eng.
	White Marrowfat	23	P. Henderson & Co.
	Elephanten	31	Haage & Schmidt
	Wachs Schwert	32	Haage & Schmidt
	Gold von Blöcksberg	34	A. D. Darbishire
	"P. Jomardi"	40	Cambridge (Eng.) Bot. Gard.
	P. elatius	41	Cambridge (Eng.) Bot. Gard.
	Prosperity	71	P. Henderson & Co.
	Pois géant sans parchemin	107	Vilmorin & Cie
	Abyssinian Black	132	S.P.I.,[2] Dept. of Agriculture
	Pisum formosum	137	H. Winkler
	Openshaw	208	S.P.I. 25439
	Archer	209	S.P.I. 22037
Light yellow	Goldkönig	30	Haage & Schmidt
	Pisum humile ?	33	A. Sutton
	Benton	138	S.P.I. 18396
	Killarney	150	S.P.I. 22078
	Khauaka	165	S.P.I. 31808

Green Cotyledons

Cotyledon Shade	Variety	Pedigree Stock No.	Source
Green to light green to yellowish green	Alaska	15	Vaughan Seed Co.
	Telephone	26	P. Henderson & Co.
	Laxtonian	27	P. Henderson & Co.
	Acacia (wrinkled)	38	W. Bateson
	Everbearing	62	P. Henderson & Co.
(Fade easily)	Yorkshire Hero	65	Thorburn & Co.
	Duke of Albany	93	Sutton & Sons
	Hundredfold	97	Sutton & Sons
	Alfred	140	S.P.I. 12888
	Blue Prussian	154	S.P.I. 19787
Yellowish green	Acacia (wrinkled)	38	W. Bateson
	Duke of Albany	93	Sutton & Sons
	Hundredfold	97	Sutton & Sons

Dark green	Market Split Pea	35	New York City Markets
	Acacia (Smooth)	39	W. Bateson
	Velocity	59	Vaughan Seed Co.
	Braunschweiger	88	Haage & Schmidt
	French Grey	149	S.P.I. 27003
	Rosenberg	161	S.P.I. 10274
	Alaska	193	S.P.I. 29366
	Scotch Beauty	198	S.P.I. 27004
	Wisconsin Blue	207	S.P.I. 22049
Green	Express	20	A. D. Darbishire
	Nott's Excelsior	21	P. Henderson & Co.
	Aldermann	28	Haage & Schmidt

yellow, yellow, light yellow, dark green, green, light green, and yellowish green, when these varieties are all grown under approximately the same conditions. Any one can distinguish between dark green and dark yellow, but one well acquainted with the color of cotyledons in *Pisum* would have difficulties in distinguishing between light yellowish greens and light yellows. The classification made is admittedly arbitrary, though based on the same sort of acquaintanceship with these colors as that of a nurseryman with varietal differences in bulbs or varietal characters in leafless nursery trees. The point which it is desired to emphasize by the foregoing remarks is that these shades of cotyledon color are distinctly *varietal* characters, and are always characteristic of the respective varieties when these varieties are all grown together under any one of the several specific[3] environments in which the pea cultures at the Brooklyn Botanic Garden have been grown.

The Relation of Environment to Cotyledon Color

One other perplexing factor enters into the study of cotyledon color in *Pisum*—the difficulty of being certain that all varieties under observation mature their seed under as nearly as possible identical environments, a factor that many geneticists experimenting with other plant forms are prone to neglect. Some varieties of peas

[2] S.P.I. stands for Office of Foreign Seed and Plant Introduction, U. S. Department of Agriculture, to which I am very much indebted for help in collecting varieties and species of the genus *Pisum*.

[3] These environments will be described in detail in a later paper.

gradually change from green to yellow when maturing, while others appear to change very suddenly, but only if plenty of sunlight and no over-supply of moisture is present. This is particularly true of some of the deep orange varieties, such as Späte Gold (P 29). The seed of this variety remains very dark green until the general appearance of the vine leads you to suppose it is ripe, but if plenty of sunlight is present and not too much moisture, and the pods are allowed to remain for a few days, the dark green changes to a very deep orange, and this deep orange is characteristic of Späte Gold when grown commercially.

With the green cotyledon varieties, one is bothered by fading of the green to a sort of washed-out yellow in many varieties, if the vines are not harvested at exactly the right time. Express, Velocity and many of the wrinkled sorts (see Hurst, 1904) are particularly subject to change under these conditions.

The above mentioned difficulties regarding the proper maturing of pea seed have been considered quite fully by Bateson, Darbishire, Lock, Tschermak and other workers in genetics. Hurst (1904) and Lock (1905) particularly have studied the tendency of certain varieties such as Telephone with green cotyledons to fade easily, even when harvested carefully, but left exposed to light. Bateson and Kilby (1905, p. 58) have studied the so-called "piebald" peas (peas with green or yellow cotyledons partly spotted or tinged with both colors) and find them to largely result from environmental conditions such as failure to ripen properly or from bleaching after ripening. "Piebald" peas are characteristic of certain varieties of peas, in which the green fades much faster upon exposure to light or moisture or to both than in ordinary green cotyledon types. "Piebald" peas of one pod, according to Bateson and Kilby, are always tinged on the same surface. Injuries causing the death of the cotyledon tissue (Bateson, 1905) (Tschermak, 1902) also are a cause of yellow spots on peas from green cotyledon varieties.

The Pigments of Cotyledon Color in Pisum

Bunyard (see Darbishire, p. 131) has shown that both yellow and green cotyledon varieties have a yellow and a green pigment in their cotyledons when the seed is immature, but the yellow cotyledon varieties possess a factor (an enzyme perhaps), which causes the green pigment to fade on the maturity of their seeds. Thus green pigment is epistatic to yellow pigment, since, when both are present, only the green is in evidence.

The Genetics of Cotyledon Color in Pisum

Historical

As early as 1729, according to Darwin (1876, I, p. 428) white (yellow cotyledon) and blue (green cotyledon) peas were found in the same pod and these results were understood to be due to chance crossing. Wiegmann, Goss (1824) and others observed that varieties of *Pisum* breeding true to blue peas when crossed with pollen from varieties breeding true to white peas, always showed a direct and immediate effect of the pollen parent. Gärtner (1849) and later hybridists incorrectly regarded this phenomenon as xenia, believing that tissues of the parent generation were affected so that the color of the seed was changed. The fact that the change in color was due to an embryonic character of a new hybrid generation seems never to have occurred to them. The true significance of these facts were never understood by Knight, Goss, Gärtner, nor any of the hybridizers before Mendel's time. Knight distinguished between cotyledon colors and seed coat colors, and Goss and others had observed practically everything regarding crosses between green cotyledon and yellow cotyledon peas except the numerical proportion of one to the other in the F_2 generation. Darwin (1876, p. 348) mentions some observations of Masters, which, if authenticated, show a complex state of affairs in the inheritance of cotyledon color, since Masters claims to have obtained both yellow (white) and green (blue)

peas from a certain pea plant and when these two kinds were planted separately each continued to produce the two kinds through four generations, that being as far as the experiment was carried. In the light of the data I present below his observations may be correct, he having possibly secured one of the yellow forms such as I have found.

Mendel (1865) found when peas with yellow cotyledons were crossed with green cotyledon forms that the first generation offspring all had yellow cotyledons, but each one of these yellow cotyledon F_1 plants produced F_2 seeds, approximately three fourths of which had yellow cotyledons and one fourth green cotyledons. Either color of parent could be used as the seed or female parent, and the result was the same. Further, the F_2 greens in F_3 only produced greens, while the F_2 yellows when planted, in some cases gave only yellows, in other cases both yellows and greens in the proportion of 3 Y : 1 G. The actual data by which Mendel supported these statements are as follows: fifty-eight crosses on 10 plants were made, and in every case, yellow was dominant to green in the F_1 generation of these crosses. 258 F_1 plants produced 8,023 F_2 seeds of which 6,022 were yellow and 2,001 had green cotyledons, an actual ratio of 75.1 yellow to 24.9 green or 3.01 Y : 1 G. Mendel is careful to call attention to the wide variability in the ratio of yellows to greens when the F_2 peas of each F_1 plant are considered separately, the variation ranging from 32 Y : 1 G on one plant to 20 Y : 19 G on another. Between these extremes, there were some among the 10 F_1 plants of which he gives the ratios, that closely approximated the theoretical 3 : 1 ratio. I call attention to this great variability that Mendel found because some geneticists of late, apparently not having noted that Mendel himself observed these same facts, have referred to this as a new phenomenon. Only average ratios from large numbers were considered by Mendel, as small numbers tended to obscure the significance of the facts. Of the 8,023 F_2 seeds secured by Mendel,

519 seeds with yellow cotyledons were used to grow an F_3 progeny. Of these, 166 F_2 seeds bred true or produced only seeds with yellow cotyledons, while 353 produced both yellows and greens in the proportion of 3 Y : 1 G. 353 to 166 gives a ratio of 2.13 to 1. Mendel (p. 327) especially calls attention to the difficulties involved in classifying the two colors of seeds, and notes, as I have done in the preceding paragraphs, that the seeds of pure green varieties and of segregate greens, have a tendency to bleach, another fact that several critics of Mendelian methods seem to have overlooked or forgotten.

Mendel's work has been substantiated by a large number of trained investigators, as well as by a host of teachers and amateurs. The results for cotyledon color in *Pisum* obtained by seven well-known geneticists are given below (Table II).

TABLE II

Hybrid Generation	Observer	Yellow	Green	Percentage of Green
Second	Mendel	6,022	2,001	24.9
	Correns	1,394	453	24.5
	Tschermak	3,580	1,190	24.9
	Bateson	11,903	3,903	24.7
	Hurst	1,310	445	25.4
	Lock	1,438	514	26.2
	Darbishire	1,089	354	24.9
Third	Correns	1,012	344	25.5
	Tschermak	3,000	959	24.2
	Lock	3,082	1,008	24.6
	Darbishire	5,662	1,856	24.7
Fourth	Correns	225	70	23.7
	Lock	2,400	850	26.1
Total		56,064	42,117	13,947	24.9

These results approximate very closely the ratio of 3 Y : 1 G demanded by Mendel's theory. Darbishire (1913, p. 62) in testing out 140 F_2 progeny with yellow cotyledons, secured 98 F_3 plants heterozygous for green and yellow cotyledons, and 42 breeding true or homozygous for yellow cotyledons, a proportion of 2.3 heterozygous F_2 plants to 1 homozygous F_2 yellow. Many varieties gathered from all over the world were used in these

[4] These data are taken from Darbishire (1913).

studies and all gave similar results. With these facts before us, there can be no denying the validity of Mendel's law as regards inheritance of cotyledon color in *Pisum*. The criticism has sometimes been made that the F_2 segregate yellows and greens were a little less green and a little less yellow owing to the association of the unit factor materials of the two pigments in the F_1 generation. In other words, segregation was not complete; the

TABLE III*a*

CROSSES OF DOMINANT YELLOW WITH GREEN (F_2 GENERATION)[6]

Crosses	Cotyledon Color	
	Yellow	Green
(P1–4 × P39–3)–1	76	34
(P21–1 × P1–1)–1	129	41
(P23–5 × P39–3)–1	60	16
(P26–1 × P1–1)–1	23	7
(P26–1 × P1–1)–2	16	0
(P26–1 × P1–1)–3	32	10
(P26–1 × P1–1)–4	34	6
(P27–1 × P1–1)–1	33	10
(P28–1 × P1–1)–1	48	6
(P28–1 × P1–1)–2	37	22
(P28–2 × P1–2)–1	46	17
(P29–1 × P35–7)–1	11	4
(P32–1 × P35–2)–1	65	16
(P34–2 × P35–7)–1	103	34
(P35–3 × P1–4)–1	9	4
(P35–3 × P1–4)–2	49	16
(P39–1 × P32–1)–1	63	17
(P40–1 × P59–1)–1	91	30
(P40–1 × P59–1)–2	68	29
(P41–1 × P21–1)–1	103	30
(P41–1 × P21–1)–2	81	25
(P62–1 × P41–3)–1	40	17
(P62–1 × P41–3)–2	74	22
(P65–1 × P41–3)–1	71	29
(P72–1 × P41–5)–1	143	54
(P72–1 × P41–5)–2	142	47
Total actually obtained	1,647	543
Total—theoretically expected	1,642.4	547.5
Ratio (theoretical)	75 yellow	25 green
Ratio (actually obtained)	75.2 yellow	24.8 green

[6] Pedigree numbers such as –1, –2, etc., following the pedigree stock number of the variety as, *e. g.*, P28–1 refer to plant numbers. P28–1, *e. g.*, is progeny plant No. 1 of stock variety P28. P28–1–1 is plant No. 1 of the second generation from pure inbred stock P28. The seed or maternal parent in a cross is always given first, *e. g.*, P28–1 ♀ × P29–1 ♂.

determiner for green pigment was not able to produce as dark a green in F_2 green segregates as in peas of the green cotyledon parent race. This is true undoubtedly in some few cases, but in still others, Hurst (1904), Darbishire (1913) and myself have been unable to find any distinction in shading by comparing the segregates with the grandparental seeds of both colors. In those cases where there has been found a difference, the observers probably failed to take into account all the environmental factors.

New Data

In my own investigations[5] on the heredity of cotyledon color, the F_1 and F_2 generations from over 79 crosses involving combinations of 40 varieties and species of *Pisum* have given results similar to those secured by other workers except in the case of crosses involving a variety of German pea, "Goldkönig," obtained from Haage & Schmidt. The data for most of these crosses are given in Tables III*a*, III*b*, III*c*.

TABLE III b

Crosses of Dominant Yellow and Recessive Yellow (F_2 Generation)[7]

Crosses	Cotyledon Color		
	Yellow	Green	Yellowish Green
(P22–3–1 × P30–A–5)–1	26	7	
(P22–3–1 × P30–A–5)–2	18	6	
(P22–3–1 × P30–A–5)–3	11	3	
(P22–6–1 × P30–A–3)–1	17	5	
(P30–1 × P1–1)–1	73	16	2
(P30–2 × P1–1)–1	51	5	6
(P30–2 × P1–1)–2	62	8	3
(P30–3 × P32–1)–1	52	10	3
(P40–2 × P30–4)–1	98	15	7
(P41–1 × P30–6)–1	49	12	1
Total—actually obtained	457	87	22
		109	
Total—theoretically expected	459.2 yellow : 106.2 green		
Ratio	13 yellow : 3 green		

[5] All varieties of peas have been inbred for at least two generations and all the ordinary precautions against differentiating environmental factors, insect pollination, etc., in use by geneticists have been employed.

[7] The investigations of Mendel, Bateson, Lock, Tschermak and others

TABLE III c

CROSS OF GREEN × RECESSIVE YELLOW (F_2 GENERATION)[8]

Cross	Yellow or Yellowish	Green
(P21–15–1 × P30–A–2)–1	2 + 1?	12
(P21–15–1 × P30–A–2)–2	4 + 1?	22
(P30–5–4 × P38–20–1)–1P	15 + 1?	30
(P30–5–4 × P38–20–1)–2P	15	13 + 4?
(P30–5–4 × P38–20–1)–1	2 + 2?	16
(P30–5–1 × P38–20–1)–1	7 + 1?	26
(P35–1 × P30–3)–1	9	22
(P35–1 × P30–3)–2	0	20
(P35–9–1 × P30–5–4)–1	1	6
(P35–9–1 × P30–5–4)–2	4	29
(P35–9–1 × P30–5–4)–3	1 + 1?	8
(P35–10–2 × P30–5–6)–1	1	12
(P35–10–2 × P30–5–6)–2	1 + 1?	26
(P35–10–2 × P30–5–6)–3	0	10
Total actually obtained, 326....	70	256
Total theoretically expected	81.5	244.5
Ratio	1 yellow : 3 green	

The variety "Goldkönig" breeds true to yellow cotyledons and wrinkledness. When crossed with varieties breeding true to green cotyledons, the F_1 generation was invariably green. In most of the crosses, the seed parent was the green variety, but reciprocals have been obtained in two cases.

The crosses were:

Goldkönig × Acacia and reciprocal
Goldkönig × Market Split Pea and reciprocal

have always shown cotyledon color in peas to be inherited independently of roundness and wrinkledness of cotyledons. The data given in Tables III b and III c give reason to believe there is linkage or partial coupling involved. Round yellow × wrinkled yellow (Goldkönig) gives practically only three classes in F_2—round yellow, wrinkled yellow, and round green. All four classes appeared in only one cross, where a single wrinkled green was obtained. Round green × wrinkled yellow (Goldkönig) gave all the expected classes except round yellow, which was absent from the F_2 progeny of all the eight crosses examined. Wrinkled yellow (Goldkönig) × wrinkled green and reciprocal gave wrinkled yellows and wrinkled greens approximating the expected ratio.

[8] The cotyledon colors of the peas concerned in Tables III b and III c were for the most part independently determined by two separate people, and these determinations when compared, differed but slightly, and only in very few cases. For help in these determinations, I am indebted to Mr. Montague Free of the Brooklyn Botanic Garden staff.

Nott's Excelsior × Goldkönig
Aldermann × Goldkönig
Scotch Beauty × Goldkönig
Sutton's Main Crop × Goldkönig

An F_2 generation has been grown from the first three of these crosses with the results (see Table III*c*) approximating a ratio of 3 G : 1 Y or the reverse of the common result. Practically all of the green seeds are distinct greens, but among those classed as yellows are several doubtful cases, and these are marked questionable. An F_3 generation is being grown which will decide whether I have erred in considering these doubtful cases as yellow cotyledon peas in which the greenish color results possibly from lack of enough sunlight during the ripening period.

When the "Goldkönig" yellow was crossed with other varieties having yellow cotyledons, the F_1 progeny all had yellow cotyledons, but in the F_2 generation, a certain proportion of peas with distinctly green cotyledons appeared, the F_2 ratio in the progeny of the ten different F_1 plants, showing considerable variation, but averaging 13 yellow seeds to 3 green seeds, provided all yellows having any considerable amount of green pigment are classified as greens. The number of F_2 generation progeny obtained was small, totaling only 566, of which 457 had yellow cotyledons, 87 distinctly green cotyledons and 22 seeds had yellowish green cotyledons. All were grown under conditions insuring their maturity, but under these conditions (greenhouse cultures) the amount of moisture present is such as possibly to cause some of the true greens to bleach. Further justification for classifying the 22 doubtful greens as true greens comes from the fact that all the varieties having yellow cotyledons used in these crosses with the exception of Goldkönig are varieties with distinctly bright yellow cotyledons, which grown under the same conditions and often side by side with the crosses, *never* show any green coloring matter in the coty-

ledons of their mature seeds. The crosses of dominant yellow with Goldkönig were:

"*Pisum Jomardi*" × Goldkönig
Goldkönig × "Mummy Pea"
Goldkönig × Wachs Schwert
"*Pisum elatius*" × Goldkönig
First of All × Goldkönig
Gold von Blöcksberg × Goldkönig
Späte Gold × Goldkönig
Benton × Goldkönig

All the yellows other than Goldkönig yellow gave the ordinary Mendelian ratios when crossed with varieties having green cotyledons. No greens were obtained from crosses between varieties having yellow cotyledons, other than those with Goldkönig.

THEORETICAL INTERPRETATION

Interpreted in Mendelian terms the above data are brought into accord with other data on the inheritance of cotyledon color in *Pisum* by regarding all varieties of peas, both with yellow and with green cotyledons, as possessing a factor for yellow pigment (Y), while the dominant yellow varieties possess a factor for green pigment (G) and a factor (I) which causes the green pigment to fade on the maturity of the seed. The German variety "Goldkönig" may be regarded as lacking both the factor for causing green pigment and the factor for causing that pigment to fade on the maturity of the seed, while the green varieties lack only the factor (I). Green pigment masks yellow pigment, hence may be regarded as epistatic to yellow pigment.

Regarded thus:

(1) YYGGII = dominant yellow varieties
(2) YYggii = recessive yellow varieties
(3) YYGGii = green varieties

Crossed with each other these give:

$(1 \times 2) = \text{YYGgIi}$ (F_1) yellow, (F_2) 13 Y : 3 G
$(1 \times 3) = \text{YYGGIi}$ (F_1) yellow, (F_2) 3 Y : 1 G
$(2 \times 3) = \text{YYGgii}$ (F_1) green, (F_2) 1 Y : 3 G

The hereditary substances responsible for yellow pigment, of course, have not been isolated and may take the form of more than one factor, but I have represented these as Y, to make my interpretation clearer. The essential point in the interpretation is that all the hereditary differences in cotyledon color in *Pisum* so far discovered may be pictured as due to the presence or absence of tw genetic factors.

TABLE IV

FACTORIAL COMPOSITION OF F_2 PLANTS OF THE THREE CROSSES AND THE APPEARANCE OF THE F_3 PROGENY

Dominant Yellow × Recessive Yellow and Reciprocals

F_2 Ratio	13 Y : 3 G	Character of F_3 Progeny
9 yellow	1 YYGGII	Breeds true to yellow cotyledons
	2 YYGGIi	3 Y : 1 G
	2 YYGgII	Breeds true to yellow but heterozygous for G
	4 YYGgIi	13 Y : 3 G
3 green	1 YYGGii	Breeds true to green cotyledons
	2 YYGgii	1 Y : 3 G
3 yellow	1 YYggII	Breeds true to yellow cotyledons
	2 YYggIi	Breds true to yellow but heterozygous for I
1 yellow	1 YYggii	Breeds true to yellow cotyledons

Dominant Yellow × Green and Reciprocals

F_2 Ratio	3 Y : 1 G	Character of F_3 Progeny
3 yellow	1 YYGGII	Breeds true to yellow cotyledons
	2 YYGGIi	3 Y : 1 G
1 green	1 YYGGii	Breeds true to green cotyledons

Recessive Yellow × Green and Reciprocals

F_2 Ratio	1 Y : 3 G	Character of F_3 Progeny
1 yellow	1 YYggii	Breeds true to yellow cotyledons
3 green	1 YYGGii	Breeds true to green cotyledons
	2 YYGgii	1 Y : 3 G

Regarded thus, the F_2 plants of all crosses so far made in *Pisum,* involving cotyledon color, can be represented by the gametic formulæ given in Table IV. The char-

acter of the F_3 progeny, *providing this interpretation of the facts regarding cotyledon color in Pisum holds,* is also indicated in this table.

Additional data on the inheritance of cotyledon color in *Pisum* will be given in a succeeding paper.

CONCLUSIONS AND SUMMARY

Variation in cotyledon color in *Pisum* belongs to all three of the categories of variation mentioned in the forepart of this paper, although there are no definite data as regards the origin of the green cotyledon and the "recessive" yellow cotyledon varieties.

1. Variations in cotyledon color due to environment are:

(*a*) Yellow cotyledon varieties producing seeds with green cotyledons, because of immaturity, absence of sufficient sunlight, excess moisture at the period of ripening of the seed, etc.

(*b*) Green cotyledon varieties, especially those with wrinkled seeds, producing seeds which fade or bleach to yellow or yellowish green owing to excess of moisture and sunlight after the seed has matured.

2. Variations due to innate or hereditary differences probably arising as mutations are:

(*a*) Different degrees or intensities of yellow and green coloring in the different varieties of *Pisum*. These different intensities are characteristic of particular varieties when all varieties under consideration are grown under approximately the same environment.

3. Hereditary distinctions as regards cotyledon color in *Pisum* may be represented by the presence and absence of two factors, a factor (I) causing green pigment to fade when the variety matures its seed, and a factor (G) causing the production of green pigment. All varieties of *Pisum* so far experimented with, have yellow pigment in their cotyledons and the determiner or determiners responsible for this pigment may be graphically represented by (Y). As the presence of green pigment masks

yellow pigment, green may be regarded as epistatic to yellow.

4. The majority of varieties with yellow cotyledons when crossed with varieties having green cotyledons, have yellow cotyledon F_1 offspring, the F_2 generation breaking up into yellow and green cotyledon plants in the ratio of 3 Y : 1 G.

The yellow cotyledon variety "Goldkönig" when crossed with green cotyledon varieties has green cotyledon F_1 offspring, in F_2 giving a ratio of approximately 1 Y : 3 G, just the reverse of the ordinary result.

"Goldkönig" crossed with other varieties having yellow cotyledons has yellow cotyledon F_1 offspring, in F_2 giving a ratio of approximately 13 yellow seeds: 3 green seeds.

With these facts in view, "dominant yellows" may be represented by the formula YYGGII, "recessive yellows" (Goldkönig) by the formula YYggii, and green cotyledon forms by the formula YYGGii. These formulæ account for all the facts so far discovered in experiments on the inheritance of cotyledon color in *Pisum,* except the data on linkage or coupling, referred to in page 539, note 7. These results will be discussed when more data are available.

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THE RESULTS OF FURTHER BREEDING EXPERIMENTS WITH PETUNIA

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IN view of the present discussion on the inheritance of doubleness in Petunia[1] and pending further investigation of the evidence in favor of an explanation based wholly or in part upon selective sterility such as has been described by Geerts[2] for *Œnothera Lamarckiana*, by Belling[3] for the Velvet "Bean" (*Stizolobium deeringianum* and other species) and by East[4] for species of *Nicotiana*, it seems desirable to make available the further results of the breeding experiments which have been carried out since the publication of the earlier data in 1910.[5] The two main facts established by the earlier work were

(1) That singles of the cultivated forms of *P. violacea*, *P. nyctaginiflora* and of various garden strains (Countess of Ellesmere, *hybrida grandiflora* and others) give only singles when self-fertilized or crossed with pollen of other singles.

(2) That these same singles give a mixture of singles and doubles in F_1 when crossed with the pollen of a double.

The later experiments carried out on the same lines and with the same kind of material have considerably widened

[1] Frost, "The Inheritance of Doubleness in *Matthiola* and *Petunia*," AM. NAT., Vol. XLIX, No. 586, p. 623, Oct., 1915; also Saunders, "Selective Partial Sterility as an Explanation of the Behaviour of the Double-throwing Stock and the Petunia," *Ibid.*, Vol. L, No. 596.

[2] "Beiträge zur Kenntniss der Cytologie und der partiellen Sterilität von *Œnothera Lamarckiana*," *Recueil des Trav. Bot. Néerl.*, Vol. 5, 1909.

[3] "The Mode of Inheritance of Semi-sterility in the Offspring of Certain Hybrid Plants," *Zeitsch. f. ind. Abst. u. Vererbungslehre*, Bd. XII, Heft 5, p. 303, 1914.

[4] "The Phenomenon of Self-sterility," AM. NAT., Vol. XLIX, No. 578, p. 77, Feb., 1915.

[5] Saunders, "Studies in the Inheritance of Doubleness in Flowers," I. Petunia. *J. of Genetics*, Vol. I, No. 1, p. 57, 1910.

the basis upon which these generalizations rest; while the fact that mixed F_1 families have now been obtained in the case of a new wild form as well as with one *nyctaginiflora* individual raised from wild seed, though not *proving* that the second statement would invariably hold good for singles of each of these two species, certainly increases the probability that this may be found to be the case.

With respect to these more recent experiments I was able in 1911 to obtain a larger series of counts than had been possible heretofore. For the opportunity to carry out the work on this larger scale I was much indebted to Professor Bateson, who kindly had some 5,000 plants grown for me at the John Innes Horticultural Institution. The results may be summarized shortly as follows:

Seven crossbred singles out of matings in which the four strains mentioned above were variously combined, were self-fertilized. *Only singles were obtained,* viz., 1,200, 123, 89, 73, 33, 32, and 12 in the different families. Total 1,562 singles.

Fifteen singles were tested by crossing and pollen from 8 doubles was used to fertilize them. The single parents included

One *violacea* plant (commercial material, new stock).

Twelve F_1 plants the offspring of 4 singles (Countess of Ellesmere) which had been crossed with pollen from various doubles (*hybrida grandiflora*). Among these 12 were 4 of those which had yielded all-single families when self-fertilized.

One *hybrida grandiflora* plant derived from a mating between two singles each of which was the offspring of a single crossed with pollen from a double.

One F_2 plant derived from an F_1 single out of the mating *nyctaginiflora* $\times$ *hybrida grandiflora* (double), the F_1 plant having been crossed back with another double.

Thus doubleness was known to have been introduced into the pedigree only once in the case of the first-mentioned (*violacea*) seed-parent, thrice in the case of the

last (F_2) plant. In the remaining 13 cases it was introduced twice,—in consecutive generations in the case of the group of 12 plants, with the skipping of a generation in the remaining instance. *Families were raised from each of these 15 plants and doubles occurred in them all.* The numbers obtained, as was to be expected from the more extended scale of the experiments, indicate a more uniform proportion of singles and doubles than was apparent in the earlier results. In many families the numbers clearly suggest a ratio of equality; in a few, however, there was a considerable excess on the side either of the singles or of the doubles. No connection could be traced between the proportion of doubles obtained and the number of times doubleness was introduced into the pedigree. The numbers in each family are shown below where the 15 seed-parents are indicated by the capital letters A to O and the pollen parents by the small letters a to h.

Parents	A×a	B×a	B×b	B×c	C×b	D×a	D×b	E×b	F×a	F×b	F×d	F×e	G×a	G×b	G×c
F_1															
Singles	27	104	74	19	27	99	58	53	250	237	148	63	103	113	78
Doubles	36	63	67	47	22	100	56	51	216	256	207	42	65	63	106

Parents	G×e	G×f	H×d	I×a	J×a	K×g	L×e	L×f	M×e	N×f	O×a	O×b	Totals
F_1													
Singles	25	188	23	58	15	34	20	25	38	51	52	17	1,999
Doubles	40	101	25	78	14	29	17	30	13	39	39	15	1,837

How far these proportions are determined, as suggested by Frost,[6] by a condition of partial selective sterility can hardly be profitably discussed until further microscopic investigations have been made, but that this explanation forms a part, though possibly not the whole, of the explanation appears highly probable. At the time it seemed advisable to postpone further breeding until wild material was available for comparison. Though repeated efforts have been made to obtain seed of wild plants, they have, in the case of *P. violacea*, been so, far quite unsuccessful. In the course of 1912 and 1913 how-

[6] *Loc. cit.*

ever, through the assistance of the authorities at Kew and of Sir Reginald Tower in Argentina, to whom I am much indebted, seed was obtained of wild plants of *P. nyctaginiflora* and also of two new unnamed wild forms (species, both white-flowered), all of which had been collected most kindly by M. Thays, director of the Botanic Garden at Buenos Aires. An entirely new stock of double material differing in nature as well as in origin from that previously employed was also now available. This was raised from

(1) seed of a plant exhibited at the Conference on Genetics held in Paris in 1911, which had some flowers double and others apparently of a normal single structure. This plant had appeared in the grounds of the establishment of MM. Vilmorin-Andrieux et Cie at Verrières-le-Buisson. Some seed harvested from the single flowers, together with a small quantity obtained from the doubles was later most courteously forwarded to me by Dr. Haagedoorn;

(2) seed sent to me by Mrs. Francis of Ventura, California, of an interesting new strain of seed-producing doubles which she had succeeded in raising.[8]

The South American seed samples gave plants of uniform type in the case of the two new forms, each presumably being a distinct species. One of the two (referred to below as P.x.), the seed of which had been collected in Cordova, was crossed with pollen from a double raised from the seed of one of the single flowers on Haagedoorn's half-and-half plant, and also with two seed-giving doubles of the Ventura strain. *Each F_1 family showed a mixture of singles and doubles.* In the case of the former cross a large number of semi-double plants with the supernumerary petaloid structures small or few in number, were also obtained. The numbers recorded are given on page 552.

These 5 seed-parents as well as other individuals tested proved quite self fertile and set a good quantity of seed when self-pollinated.

[8] For an account of this strain see Mrs. Myrtle Francis [Shepherd] on "Double Seeding Petunias," *J. of Heredity*, Oct., 1915.

Single Parent	Double Parent	F_1		
Flowers White	Flowers Magenta	Flowers Magenta		
		Singles	Semi-doubles	Doubles
P.x. 1....	Descendant of Haagedoorn's plant....	15	54	23
P.x. 2....	" " "	12	32	15
P.x. 3....	" " "	5	32	4
Totals		32	118	42
	Flowers Rose Pink	Flowers White with Dark Tube		
P.x. 4....	Ventura plant 1.....	14	—	15
P.x. 5....	" " 2.....	3	—	2
Totals		17	—	17

Thus we have evidence that in a third species (for as such there seems good ground for regarding this wild type) doubles appear in F_1 when a cross is made with a double form. The behavior in this respect of the other new form has not yet been ascertained.

With regard to *P. nyctaginiflora* the seed of which was collected from Punta Ballena, Maldonaldo (Uruguay), it was noticed that the plants were not entirely uniform in color, some showing a very definite tinge of purple on the outer side of the flower tube, others scarcely a trace. Similar variations had also been observed in the original (1906) commercial material. Whether this variability is normal to the species or is an indication of crossing is not certain. It is somewhat remarkable that in this original material all the 8 individuals tested proved to be self fertile and yielded abundance of seed, whilst six self-pollinated flowers on three of the Uruguay plants taken at random did not yield a single seed. It seems unlikely that this result could be due to accident, or to a difference of conditions due to the fact that the 1906 plants were grown in the open, whereas the individuals grown from the wild seed were kept in pots in a cool house. Indoor treatment had not been found to affect the fertility of the other strains, and it is hardly likely that it did so here; but this point is now being verified. Only one Uruguay plant was crossed with pollen from a double (Ventura 2). From this cross the same result was ob-

tained as with the commercial material. *F_1 was mixed,* the numbers recorded being 225 singles and 113 doubles.

So far, then, the material employed has furnished no exception to the statement that singles crossed with the pollen of doubles yield some doubles in F_1 though breeding true to singleness when self-fertilized or pollinated by other singles.

Unfortunately very little evidence is yet available as to the results of using the double plant as the seed-parent. Haagedoorn's plant was of an exceptional character and the Ventura plants, though more typical, showed considerable sterility. Only 5 plants were raised from the seed sent by Mrs. Francis. These were all double. Only one individual was obtained by self-fertilization of these plants and this was also double. A cross with a single (Countess of Ellesmere) produced only one offspring and this plant was lost before flowering. It is however hoped by a repetition of this mating to obtain an F_1 generation which will throw further light on the relation of the double to the single.

The following information received from Professor Bateson concerning a cross made at the John Innes Horticultural Institution by E. J. Allard unfortunately only came to hand after the above account had been forwarded for publication. In the mating in question a *nyctaginiflora* plant, one of a batch raised from a sample of the same wild seed as that from which my own plants were grown, was crossed with pollen from a pink-flowered double, a florist's highly cultivated type of plant. *More than 20 plants were raised in F_1 and all were single.* If we consider this number large enough to be taken as conclusive we should have in this experiment an exception to the results hitherto obtained and summed up in the general statement formulated above. We must then suppose that there exist in these *Petunia* forms certain singles and doubles the relation between which is such that doubleness completely disappears in the F_1 generation obtained from a cross between them.

INHERITANCE OF SEX IN THE GRAPE[1]

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SINCE the discovery of Correns in 1907 that in *Bryonia* the staminate plants produce two kinds of gametes with respect to sex, and the pistillate and hermaphrodites only one, great advances have been made in the study of sex inheritance.

Shull (1910, '11, '14) has shown that in *Lychnis dioica* also the staminate plants are heterozygous for the sex genes, while the pistillate ones are homozygous, but that the hermaphrodites are heterozygous for the determiner for femaleness and for the hermaphrodite condition. These hermaphrodites were apparently developed from staminate plants as they bear only partially developed pistils in many flowers, and further, the factor for narrow leaves is linked with the determiner for the hermaphroditic condition, while in the normal males it is linked with that for maleness, as pointed out by Shull. Apparently the determiner for femaleness is carried suppressed and linked with the determiner for maleness in the staminate plants.

A simpler case of sex inheritance than either of the above is that of the sweet pea in which Bateson has shown that genotypically three kinds of plants may be produced; namely, the normal hermaphrodites, which produce only hermaphrodites when selfed, the pistillates bearing contabescent anthers, which when pollinated with pollen from the normal hermaphrodites produce the third type, which is phenotypically the same as the normal hermaphrodites. These when selfed produce hermaphrodites and pistillate plants in a 3:1 ratio, showing them to be heterozygous for

[1] Presented before the Society for Horticultural Science, Ohio State University, December, 1915.

the hermaphrodite and female determiners, and showing further that in the sweet pea only one dose of maleness is necessary for the production of functional stamens.

Similarly in many animals, it has been proved by Wilson, Morgan and others that the males are heterozygous for the sex determiner and the females homozygous, and that this condition is correlated with the presence of two chromosomes in the female which are distinct from the others and which they called the "X" bodies, while in the male only one may be present, or if there are two, the second is sometimes smaller and is spoken of as the "Y" body. Occasionally the X and Y bodies may be of equal size and the supposition that they are different is based upon inheritance studies.

The reverse of the above mentioned condition may exist, as in *Abraxis,* pigeons, cultivated fowl, etc., in which the males are apparently homozygous for the sex determiner and the females heterozygous.

Strasburger found that in *Bryonia* there were two chromosomes which were larger than the others and thought that these might carry the determiners for sex.

A great deal of evidence has recently been collected which points to the chromosomes as being the carriers of factors and as many factors have been shown to be linked with sex, it seems safe to conclude that certain chromosomes carry the determiner for sex. If this is the case, then in the hermaphroditic plants it must be assumed that the determiners for maleness and femaleness are linked or carried in the same chromosome; otherwise there would continually be produced not only hermaphrodites but staminate and pistillate plants as well.

The trend of development in many plant groups seems to be toward the production of a diecious condition by the suppression of the stamens in one set of individuals and of the pistils in another. As an instance of this may be cited the strawberry, in which staminate, pistillate and perfect flowers are produced. The grape and maple and many other plants show a like suppression in varying degrees.

Because of the number of flower types, and the fact that most of our cultivated grapes are only one or two generations from the wild, they would seem to furnish ideal material for the study of sex inheritance.

Two types of vines are found in the wild, those producing functionally pistillate flowers, but bearing reflexed non-functional stamens, and those producing functionally staminate flowers, but bearing suppressed pistils.

We have then apparently a transitional form, in the case of the grape, from a hermaphroditic condition such as is found in the apple, in which the male and female determiners are apparently linked, to the strictly diecious forms, as ashes, willows, etc., in which the determiner for maleness is completely suppressed in the sex chromosome bearing the determiner for femaleness, and the female determiner is completely suppressed in the chromosome bearing the factor for maleness.

On this hypothesis we would assume that in the functionally pistillate grape flowers the suppression of maleness has begun and evinces itself in the production of reflexed stamens bearing non-functional pollen, *i. e.*, lacking germ pores (Dorsey, 1913) and containing degenerate generative and vegetative nuclei embedded in apparently normal cytoplasm[2] (Gard, 1913). The period of degeneration of the nuclei is not at all definite. Rarely, the microspore nucleus does not divide. In some cases degeneration takes place directly following the microspore division, in others one nucleus only will degenerate at this time, and in still other cases the two nuclei will appear normal at the time of dehiscence (Dorsey, 1913). Beach (1899), Booth (1902) and Hedrick and Anthony (1915) have shown from pollination and germination tests that occasionally a few pollen grains borne in reflexed stamens are entirely functional. There is an apparent lack of suppression of maleness, occasionally, which allows the development of these normal grains.

Similarly it might be assumed that in the staminate

[2] Pollen of this type should not be confused with abortive pollen which is often produced in hybrids.

flowers suppression of the female determiner has taken place. Booth (1902) and Dorsey (1912) have shown that in practically all staminate grape flowers suppressed pistils are found. In some cases under cultivation and in rare instances in the wild state, the suppression of pistils is less marked and fairly well developed to perfectly developed pistils are formed. On individual plants occasionally all gradations from staminate to functionally hermaphroditic flowers are found.

A third type found under cultivation but which is extremely rare in the wild, is the functional hermaphrodite bearing all hermaphroditic flowers. A discussion regarding the probable origin of this type will be taken up later.

Although breeding work has been carried on for the past twenty-five or thirty years in this country with the grape, apparently little attention has been given to the inheritance of the various flower types, although a knowledge of sex inheritance would be of much value to the breeder. In 1914 Anthony published valuable data on sex inheritance in the grape, but gave no satisfactory interpretation of the results. In 1915 the data again appeared in more detail (Hedrick and Anthony, 1915), and, as no further attempt was made to interpret the results, the writer wishes to present the following as a probable explanation of sex inheritance in the grape, or at least as a working hypothesis for the interpretation of further results which may be obtained.

For the reason that in diecious plants there are apparently definite determiners for maleness as well as femaleness, while in animals it is supposed that males are produced when only one dose of the sex determiner is present, while females are produced if two doses are present, it seems well to use different symbols to designate the sex determiners of plants from those of animals. Therefore, those suggested by Shull (1914, p. 293) in which "the female is assumed to be a neutral homozygote," will be used in the following discussion, namely FF to represent a female and FM to represent a male.

The hermaphrodites would then be designated as $\widehat{FFM}$ or simply as FH. It will be seen from the following discussion that the only formulation which will meet the conditions is that which assumes the female to be a neutral homozygote.

In the above mentioned paper on the "Inheritance of Certain Characters of Grapes" (Hedrick and Anthony, 1915) the authors have concluded that the results obtained on inheritance of sex do not conform to the explanation of sex inheritance dependent on one sex being considered heterozygous and the other homozygous for sex determiners. It appears, however, that by using the hypothesis of partial suppression of sex determiners, the condition in the grape would be in accordance with the assumption of a homozygous condition for femaleness in the functional females, a heterozygous condition for maleness and femaleness in the functionally male plants, and a heterozygous condition for femaleness and hermaphroditeness in some of the hermaphrodites, while others would be homozygous for the hermaphrodite determiners. The authors based their conclusions upon the supposition that the hermaphrodites bearing upright and those bearing reflexed stamens were of a single type genetically, and produced only hermaphrodites and no females when crossed. This assumption seems erroneous.

Using the formulæ suggested above, let us apply them to the data given by the authors, which are as follows:

U × U[3] = 180 U + 47 R	R × R[3] = 16 U + 16 R
U selfed = 673 U + 152 R	R selfed = 94 U + 73 R
U selfed = 18 U + 0 R	
Total ..... 871 U + 199 R	Total ..... 110 U + 89 R
Ratio ..... 4.3 U : 1 R	Ratio ..... 1.2 U : 1 R

R × U = 207 U + 206 R
Ratio .... 1 U : 1 R
U × R?

Hermaphrodite female × pure male = 56 hermaphrodites + 51 males.

[3] "The pollen parent is always placed last." "U" refers to hermaphrodites bearing upright stamens which are usually functional. R refers to hermaphrodites bearing reflexed stamens which rarely produce functional pollen.

In the following discussion the term "female" will refer to the plants bearing morphologically perfect flowers but having reflexed stamens, the pollen of which is not functional. "Hermaphrodite" refers to those bearing perfect flowers, the stamens of which are upright and produce functional pollen. "Male" refers to those plants bearing staminate flowers.

The expectation from the cross "U × U" (hermaphrodite FH × hermaphrodite FH) would be 3 hermaphrodites: 1 female (FF); the hermaphrodites being of two types, viz., 2 FH:1 HH. This ratio is very closely met in the figures 180 upright and 47 reflexed. "U selfed" should give the same proportions and these are closely approached in the figures 673 upright and 152 reflexed. This assumes the production of homozygous hermaphrodites (HH), which, when either selfed or crossed with other types, produce only hermaphrodites. Apparently the two hermaphrodites which produced 18 hermaphroditic seedlings only, when selfed, are of this genetic constitution. At the Minnesota Experiment Station four hundred seedlings of Beta, open to cross pollination, produced only hermaphroditic flowers; indicating that Beta must be homozygous for the hermaphrodite determiners.[4]

The crosses "R × R" and "R selfed" (female FF × female FF), producing both hermaphrodites and females, might be explained on the hypothesis already given, viz., that of partial suppression of the determiner for maleness in the chromosome bearing the determiner for femaleness.

It has already been pointed out that in the pistillate flowers bearing reflexed stamens, a series of pollen conditions, ranging from those in which the microspore nucleus does not divide, through those in which the generative nucleus aborts directly after the microspore division, to those in which a few normal functional pollen grains are

[4] In *Lychnis dioica* Shull has shown that homozygous hermaphrodites are never produced.

produced, has been found. This very evidently shows that variation in the amount of suppression of the determiner for maleness takes place in the determiner for sex of these normal grains. This normal pollen when used to pollinate pistillate flowers should give, in some cases, females bearing reflexed stamens and in others hermaphrodites, depending upon the extent to which suppression of maleness is lacking in the chromosome bearing the sex determiners of these normal pollen grains.

From the cross "R × U" (female FF × hermaphrodite HF) should be expected females (FF) and hermaphrodites (HF) in the proportion of 1:1. This ratio is met exactly in the cross "R × U" = 207 upright and 206 reflexed.

The following analysis, kindly furnished me by Mr. Anthony of the New York State Agricultural Experiment Station, of the cross "hermaphrodite female × pure male" which produced "56 hermaphrodites + 51 males," shows that both hermaphrodites and females were used as the female parent and that three kinds of males were used, namely, wild males, males one generation from the wild and "intermediates" (males bearing occasionally a few well developed pistils).

	Upright	Reflexed	Males
Hermaphrodite × wild male	7	6	9
Hermaphrodite × male (1 generation from wild)[5]	15	0	14
Female × male (1 generation from wild)[5]	10	3	7
Hermaphrodite × intermediate (origin unknown)	6	4	15
Female × intermediate (origin unknown)	0	1	3
	38	14	48[6]

The various combinations will be considered separately.

The cross hermaphrodite (FH) × wild male (FM) produced 7 hermaphrodites, 6 females and 9 males, somewhat approximating the expected ratio of 1 female (FF) : 1

[5] The result of hermaphrodite × wild male.

[6] These totals do not quite coincide with those given in the published data, as the parents of 7 of the vines were not certainly known and are therefore omitted.

hermaphrodite (FH) : 2 males (FM) and (MH). The male MH is an entirely new genotype but apparently can exist as shown by the next cross, in which a hermaphrodite was pollinated by a male derived from this cross. Fifteen hermaphrodites, no females and 14 males were produced, the expected ratio being (if a male of the type HM were used) 2 hermaphrodites (HF and HH) : 2 males (MH and MF). If a normal male of the constitution FM had been used on a hermaphrodite of the constitution HF we should expect to have produced 1 hermaphrodite (HF) : 1 female (FF) : 2 males (HM and FM). No females were produced. Again we might assume that the hermaphrodite used was of the constitution HH and that a normal FM male was used. In this case we should expect a 1 : 1 ratio of hermaphrodites and males as before, but in this case all of the males would be of the new type HM. It seems, therefore, that the production of this new male genotype (MH) must be admitted. Further evidence for the production of males of this type is produced in the cross female (FF) $\times$ male (one generation from wild) which produced 10 hermaphrodites, 3 females and 7 males. If the males used had been of the normal type FM only females and males could have been expected, as are found under wild conditions, and no hermaphrodites. If a male of the type HM were used, however, the expected ratio would be 1 hermaphrodite HF : 1 male FM. The presence of three females, although not expected, from the cross FF $\times$ HM can be readily explained, as it has already been pointed out that the males "one generation from the wild" are of the two genotypes FM and HM, but of one phenotype, and therefore could not be distinguished at the time of pollen collection.

The cross hermaphrodite $\times$ intermediate (origin unknown) which produced 6 hermaphrodites, 4 females and 15 males, throws some light on the genetic constitution of these intermediates and incidentally upon the suppression of femaleness. Observations on a number of "intermediates" produced at the Minnesota Fruit Breeding

Farm showed that certain clusters of a vine may be entirely staminate, while others of the same vine contain all gradations from staminate to functionally perfect flowers, many of which are capable of setting fruit. There is very evidently a suppression of femaleness in certain parts of these plants and not in others. This raises the question as to whether pollen from the pure staminate clusters can transmit only determiners for maleness and femaleness, or whether they are able to transmit the hermaphrodite condition. Mr. Anthony informs me that the pollen used in the above cross was "most certain to have come from such blossoms" (*i. e.*, from pure male clusters). If the two types of gametes produced by these flowers bear the determiners H and F. respectively, the cross hermaphrodite $\times$ intermediate should produce hermaphrodites and females in a 3:1 ratio and no males, while if these male flowers function as normal males and the gametes produced carry the determiners F and M respectively, a ratio of 1 hermaphrodite (HF) : 1 female (FF) : 2 males (HM and FM) would be expected. A close approximation to this ratio was actually produced.

The cross female (FF) $\times$ intermediate which produced 1 female and 3 males, gives further evidence that the staminate flowers of the intermediate vines do not produce gametes bearing the hermaphroditic determiner, but act as pure males. Otherwise the appearance of the three males can not be explained.[7] Although the number of vines produced from this cross is small, still the appearance of the three males is extremely significant.

It has already been pointed out that in the wild there are two types of vines, male and female, and that under cultivation a third type, the functional hermaphrodite, is common. We are now in a position to discuss the possible origin of these types. It is clear that both the staminate and functionally pistillate vines carry the determiners for femaleness and maleness, respectively,

[7] Anthony (1914) pointed out the fact that the pollen from these intermediates "seems to behave as the pollen of a pure male."

partially suppressed and therefore, there are two possibilities with regard to the origin of functional hermaphrodites. (1) Maleness may express itself fully in one of the chromosomes bearing the determiner for femaleness in a pistillate plant, and (2) femaleness may express itself fully in the chromosome bearing the male determiner in the staminate plant. I think it can be said definitely that functional hermaphrodites have been developed in both of these ways. The production of hermaphrodites from the cross female × female can hardly be explained on any other basis than entire lack of suppression of maleness in certain gametes bearing the female determiner, while the appearance of well-developed pistils in a few flowers of certain male vines must be the result of lack of suppression of femaleness in at least a portion of the somatic cells of these males.

As there is an apparent segregation in the somatic tissue of these vines, whole clusters and occasionally all clusters on a cane being staminate while others bear many intermediate and perfect flowers, it seems logical to assume that the perfect flowers can transmit the hermaphroditic condition to some of their seedlings through both the male and the female gametes, resulting in either homozygous or heterozygous hermaphrodites, all of whose flowers are perfect.

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ON PRIMARILY UNADAPTIVE VARIANTS[1]

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THIS paper deals with vertebrate *variants* (forms or species of animals more or less related but differing from one another) which, although geographical, are not direct or obvious responses to the environment.

Several types of variants are defined. Representative forms occupying adjacent regions are designated as *adjacent* races or species: Forms intermediate in structure between adjacent forms and occupying territory remote from them as *foreign intermediates:* Related forms occupying the same territory and contrasted in superficial characters as *complements:* Forms separated geographically and showing greater resemblance (not induced by environmental adaptation) than their degree of relationship would presuppose, as *outcrops.*

The hypothesis is advanced that, probably on account of competition, closely related forms are antagonistic.[2] That is, when in touch geographically they tend to force one another apart in superficial characters. If this hypothesis, which seems to fit into certain known facts extremely well, be accepted, it involves a centrifugal force in Evolution opposed to the centripetal tendencies of blood relationship.

It is the main theme of the paper to advance the concept of these two forces as the fundamental framework of evolutionary control, the helm which is swayed by natural selection or other forces.

Larus marinus (the great black-backed gull), which

[1] Paper read before the Section of Biology of the New York Academy of Sciences, February 14, 1916.

[2] See Darwin, "Origin of Species," p. 57. "We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature."

breeds in the north and reaches our latitude only in winter, finds its nearest relative not in an equatorial species, but in *Larus dominicensis* of the southern hemisphere, below 10° south latitude. This bird is more or less of an intermediate between *Larus marinus* (the great black-back), and *Larus fuscus* (the lesser black-back) which occurs with the former in Europe and is represented by allied forms eastward to the Pacific coast of North America, the mantle of *dominicensis* is very dark as in the larger bird; its size about that of the lesser ones. These are four in number—*Larus fuscus* occurs in Europe east to the Dwina, *Larus affinis* from the Dwina eastward across Asia, *Larus schistisagus* in northern Japan and Bering Sea, *Larus occidentalis* on the west coast of the United States. The four birds of this series are most readily separated by size and proportions of feet. *Affinis* resembles *schistisagus* in the former, *fuscus* in the latter; *schistisagus* resembles *affinis* in the former, *occidentalis* in the latter. That is *affinis* and *schistisagus* are more or less intermediates structurally between the species they separate geographically. For convenience we will call them "adjacent intermediates" as opposed to *dominicensis* which we will call a "foreign intermediate" between *marinus* and birds of *fuscus* group.

A species of vertebrate animals distributed over a wide geographical area often varies in the different regions it inhabits sufficiently to be separable into different intergrading races. Ordinarily no two of these races from the very nature of their origin will be found inhabiting the same region, sometimes they mingle in migration. Often these races are in direct response to different environmental conditions, but sometimes this response can not be traced. Such races form a series comparable to the gulls of the *Larus fuscus* group, and we may call them "adjacent races" and the gulls of the group referred to "adjacent representatives," also we may call *Larus dominicensis* a "foreign representative" of the

black-backs as well as a "foreign intermediate" between the two divisions of that group.[3]

Many of the smaller gulls have a well-defined dark hood in the adult. These hooded species may be divided into two apparently natural groups, the first in which the hood is black, the second in which it is dark brown. In the former group Bonaparte's gull (*Larus philadelphia*) has a great deal of white in the primaries, making a lengthwise band in the wing, conspicuous in life. Bonaparte's gull is found in North America. In the brown-headed *Larus ridibundus* of Europe and Asia the white in the wing makes a similar conspicuous mark, so that no one seeing the two species in life could fail to note the great resemblance. They show distinctly what is ordinarily termed parallelism. Such more or less distantly related, geographically separated parallels, not environmental parallels, are of not infrequent occurrence. For convenience we will call them "outcrops."

Probably the closest relative of *Larus philadelphia* is *Larus saundersi* from the inland waters of China and Mongolia, visiting the coast in winter. This would be a foreign as opposed to an adjacent representative.

Using, for the sake of familiarity, some of the same material we have already considered, if we contrast white-winged *Larus philadelphia,* which is common in the vicinity of New York, with its closest relative common here, the laughing gull *Larus atricilla,* we will find that the two are as different as the limits of the natural black-hooded group of which they are both members will allow. The white primaries of *philadelphia* are contrasted with the unusually dark primaries of *atricilla,* the mantle of the former is pale, that of the latter dark, and there is considerable difference in size. Such contrasted co-existing allies are of frequent occurrence, let us call them "complements."

For my next example I will turn to an entirely different group of animals, the Spanish mackerels, fishes of the

[3] See Matthew, W. D., *Ann. New York Acad. Sci.,* 1915, Vol. XXIV, p. 180, "Principles of Dispersal."

genus *Scomberomorus,* found in warm seas of the world. Along the Atlantic coast of America *S. maculatus* is abundant south to Florida, and *S. regalis* is abundant about Cuba, where *maculatus* is practically unknown. *Regalis* is a close ally, we may reasonably say a derivative of *maculatus,* from which it differs in the scaling of the fins, arrangement of the numerous brownish spots which ornament both species, and in minor characters. Occurring abundantly between the two and associated with one to the north, the other to the south, is unspotted *S. cavalla* (the kingfish of Florida), I will call such an interposed species an "intrusion." Incidentally *cavalla* is a complement of both *maculatus* and of *regalis.*

All the above mentioned cases of variants have this in common: although more or less geographical they are not obvious and direct responses to the environment; probably environment has little to do with them. Apparently we get all the various types of variants as classified where such control is lacking or not essential. It is then pretty certain that variants occur when not induced by environment. Lacking contrary evidence this hypothesis is accepted, and cases where it apparently obtains are alone considered in this article, environmentally induced variants being too common and too generally discussed to need treatment here.

Let us go over the various types of variants, beginning with the simplest, and discuss them in relation to their probable origin. The admittedly inherent tendency to variation in any form would be sufficient, where the form is widely distributed, to break it up into adjacent races. Adjacent representative species are pretty obviously derived from adjacent races. Even temporary isolation so readily explains this slight advance and is so easily assumed, that perhaps we should look no further for explanation. So far we have trodden familiar ground scarcely worthy of mention, and the hypothesis, that namely, probably on account of competition, closely related forms are antagonistic, is conservative enough.

If this hypothesis which seems to fit into the known facts with surprising neatness, be accepted, the writer believes that it will explain a force in direct opposition to the commingling of blood along a line of geographical demarcation of adjacent races, tending to drive those races apart in structure and making possible the derivation from them of adjacent species without geographical isolation. In fact we find in the incompatibility of closely related forms a powerful centrifugal force for differentiating species and forcing them apart[4]—and it also explains complementary coexisting forms, as it would tend to make coexisting forms complementary and would not act to change or eliminate them if they already were so. In the case of the foreign intermediate we have a geographically isolated form less influenced by the centrifugal forces, therefore varying less, retaining intermediate or primitive characters. This centrifugal force should always be considered as balanced against blood-relationship, doubtless the chief cause of resemblance in species. In the outcrop we have a case where the centrifugal force is inoperative and the centripetal tendency brings about a parallelism different in fundamental nature from the more familiar environmentally induced parallels.

There seems to be an analogy between the outcrop and homologous rectigradations in Paleoevolution.

Having given this rather concentrated outline of my hypothesis and the class of facts it is designed to explain it will not be out of place to mention other widely scattered examples of the important classes of variants alluded to. I will begin with the foreign intermediate.

Trichiurus is a long band-like silvery fish with a filamentous tail found along the shores of warm seas, where also occur numerous representatives of the Scombroid or mackerel-like fishes. The two are utterly unlike, yet a clear line of relationship is found through intermediate forms (for instance *Lepidopus*) from the ocean depths.

[4] See, however, Gulick, J. T., "Evolution, Racial and Habitual," 1905, p. 258.

Lepidopus and its confreres are a foreign intermediate family between the mackerels and *Trichiurus,* as *Larus dominicensis* is a foreign intermediate species between the two closely related types of black-backed gull in the north. Please note another analogy. The fundamental philogenic Scombroid characters of *Lepidopus* are a direct response to life at the surface of the mackerel group. Though an intermediate it is impossible (as it is difficult in *Larus dominicensis*) to believe that it occupies the primitive habitat of the group. Other fishes which have persisted in regions distant from the center of ichthyological competition, namely the marine shore line, as in the deep sea or in fresh waters, are in a sense foreign intermediates. Before leaving *Trichiurus* let us glance at its ancestry. The deep-sea *Lepidopus*-like fishes would have little chance in competition with the mackerels in surface waters. They form in a sense a rectigradation (again apologies to Paleontology) development from the mackerels of which *Trichiurus* is the terminal member; but *Trichiurus* is so unmackerel-like that it may and does inhabit the same waters with the mackerels; it is broadly speaking complementary to them.

The tree squirrels are connected with the ground inhabiting spermophiles through the chipmunks (*Eutamias, Tamias* and *Callospermophilus*). Our common eastern chipmunk (*Tamias*) is a boldly marked animal in appearance very much resembling the Rock Squirrel (*Callospermophilus*) of high altitudes of the northwest. The resemblance is more striking than the closeness of blood relationship would presuppose, and *Callospermophilus* may be characterized in this connection as an outcrop. The forms of *Eutamias* inhabiting the same regions as *Callospermophilus* and sometimes found associated with it, are very unlike that animal, and form a very good complement with it. The eastern chipmunk is a foreign intermediate in superficial characters between *Callospermophilus* and western *Eutamias.* Interlocking

of foreign intermediate and outcrop in this case is interesting, it may or may not be significant. Inhabiting more or less the same region as *Callospermophilus,* as do western *Eutamias,* are other spermophiles. They are however speckled or plain colored, little marked for the spermophile group, complements of it, whereas widely separated from it, to the south and east occur spermophiles with sufficient striping to perhaps be considered foreign intermediates between these two northwestern types of spermophile. The above discussion will show how in a single group of mammals, ground squirrels, there exist the various types of variants which have been differentiated above in discussion of fishes and birds.

The most favorable region for fish development and the center of evolutionary competition for fishes is the tropical coral reef. A great many species have the habit of seeking protection among the projections and crevices which there occur in abundance, and these as a rule are very brightly colored, blue, yellow, green, red, or marked with bold bizarre patterns in endless variety. The theory has been advanced and quite generally accepted that the colors harmonized with the brightly colored corals, etc., over which they occurred, but the fact seems to be that although with occasional spots of color the tone of the reef as a whole is comparatively uniform, these bright-colored fishes are very conspicuous swimming over it, in fact give it a good deal of its brilliant appearance. Butterfly fish, wrasses, chromids, parrotfish, etc., belong to this bright, varied crowd. They are safe from all enemies among the labyrinths of the reef and in their evolution have not felt the necessity for concealment.[5] Neutral tones are closer the one to the other than the bright and bizarre, therefore from centrifugal force we should expect, as we find, the bright and bizarre.

Brilliant birds amidst a luxuriant foliage simulate the conditions and the security of reef fishes and frequently

[5] Reighard, J., Public. Carnegie Instit., Washington, 1908, No. 103.

have similarly bright and striking plumage, especially in the males, though the sitting females may be dull. The bright colors of the males may readily have been acquired under control of similar forces. I do not mean to rob sexual selection of its reputed force, but indications are that it is not entirely responsible for all that might be laid to its door. The genus *Dendroica* of small active arboreal birds has developed numerous bright, varied and beautiful colors. Two species perhaps as closely allied as any others are the Blackpoll *Dendroica striata* and Bay-breasted warblers, *Dendroica castanea.* It is interesting to find them very fair complements, the one of the other, in plumage of the breeding male, though females and young are little different; whereas the male blackpoll resembles in color the black and white warbler, *Mniotilta varia,* a distantly related bird of the same family.

Ten years ago the writer had the pleasure of making the acquaintance of the beautiful grey slender-billed fulmar (*Priocella*), on the southern ocean. Sometime afterwards when crossing the North Atlantic he met with the northern fulmar (*Fulmarus*) and was surprised to find the resemblance between the two so great, even carried to a light mark on the wing, very useful in field identifications. Though belonging to the same family the two species are really not very closely allied and are an example of the outcrop. Another case which might be so considered is that of the African true larks or pippits which simulate our meadow larks of the family Icteridæ in color. All passerine birds are so closely allied that the two are not too distantly related to be outcrops, but there are other reasons for thinking that this case is not a very good one, but rather a case of environmental parallelism. The black breast mark, for instance, is so common among ground birds that it probably has concealing value.

The isolated islet of South Trinidad in the south Atlantic is remarkable in that three closely related species

of petrels (Genus *Æstrelata*) are indigenous to it. These are almost identical in size and build but differ markedly in color. *Æstrelata arminjoniana* is bicolored, dark above and white below, *Æstrelata trinitatis* is uniformly dark colored, *Æstrelata chionofara* resembles the former bird, but the white of the underparts spreads up the sides of the neck and on to the back, which is largely white, with dark shafts to the feathers. These birds are obviously very closely related and it is sometimes debated whether or not they are distinct species or merely color phases of one and the same thing.[6] The most convincing evidence, in favor of the hypothesis of distinctness perhaps being that *arminjoniana* and *trinitatis*, forms which have long been known to science, seem to breed on the islet at somewhat different times of the year. *Chionofara* has only recently been described and is so far known from the type specimen only.

The writer has been particularly interested in these birds and has studied them carefully with a view to forming a definite opinion as to their relationship. The bicolored type of plumage represented by *arminjoniana* is perhaps the most common in the cosmopolitan pelagic genus *Æstrelata* of which it is a member, but *arminjoniana* is separated from most of the genus by the greater development of dark color on the side of the neck forming a sort of dark collar. Several uniformly dark colored *Æstrelata* also occur in various parts of the world, comparable to *trinitatis*. The third and recently described form is complementary in color to *trinitatis*, being very white for the genus, and complementary in pattern to *arminjoniana*, having the side of the neck white instead of unusually dark.

If we had three recently evolved forms breeding on the same islet, complementary plumage is what would be expected, and that the three types of *Æstrelata* from there show such plumages is good evidence that they are bona fide forms, not color phases.

[6] Murphy, R. C., *The Auk*, July, 1915, XXXII, No. 3, pp. 342–344.

What color phases are is a matter aside from the thread of the paper but the consideration of this case has led so close to the interesting unsettled problem that the writer hopes to be pardoned for calling attention to certain things about them which he has noticed and which seem to hold good pretty well. First, they are limited to about four manifestations. The timber wolf, *Canis occidentalis* we are told is gray, white, black, or red. The gray squirrel (*Sciurus carolinensis*) is gray or black. The black bear (*Ursus americanus*) black (normal), white (glacier bear) or red (cinnamon bear). The red fox (*Vulpes fulvus*) gray (cross fox), black (silver fox) or red (normal). The screech owl is gray or red.

Students of heredity have shown that the normal gray coat of a wild guinea pig is a composite of black, white and red, which has been broken down by breeding into its constituent parts so that we get black guineas, red guineas, white guineas and guineas with the colors in patches. The colors, you will notice, are the same as those of the color phases occurring in nature and it seems probable that color phases have come about by a similar breaking down and reduction of the normal colors in a species, and have definite limits beyond which they are not likely to go.

In conclusion one might go on indefinitely demonstrating the application of the rough classification of non-adaptive variants proposed in our initial paragraph, limited only by the number of forms one could call to memory. If the significance of the classification has not been exaggerated it is difficult to find another theory which fits as well with the existing phenomena as the one advanced of a centrifugal force, though it is a pure theory and its acceptance a matter of individual taste.

SHORTER ARTICLES AND DISCUSSION

TABLES OF LINKAGE INTENSITIES

In the July, 1916, NATURALIST, Professor Emerson gives convenient formulæ for calculating linkage intensities. His formula (I) is especially useful because it is applicable either to cases of coupling or to cases of repulsion. I had independently worked out empirical formulae for calculating coupling and repulsion which are very similar to that given by Emerson; indeed they are identical with it, if 1 is substituted for r in cases of coupling and for s in cases of repulsion. I had failed to observe, what Emerson shows, that the two formulæ may be given a single generalized form.

TABLE I

THE F_2 RATIO, 9: 3: 3: 1, AS AFFECTED BY COUPLING OR LINKAGE, A AND B ENTERING THE F_1 ZYGOTE IN THE SAME GAMETE

Ratio, Cross-over to Non-cross-over Gametes	Proportion Cross-over Gametes	F_2 Zygotes				
		AB	Ab	aB	ab	Total
$1:x$	$\frac{1}{x+1}$	$3x^2+2(2x+1)$	$2x+1$	$2x+1$	x^2	$(2x+2)^2$
1:1[1]	1/2	9	3	3	1	16
1:2	1/3	22	5	5	4	36
1:3	1/4	41	7	7	9	64
1:4	1/5	66	9	9	16	100
1:5	1/6	97	11	11	25	144
1:6	1/7	134	13	13	36	196
1:7	1/8	177	15	15	49	256
1:8	1/9	226	17	17	64	324
1:9	1/10	281	19	19	81	400
1:99	1/100	29,801	199	199	9,801	40,000
Limiting values[2]		3	0	0	1	4

I had also found it convenient, for my own use, to make out and enter in my notebook tables of equivalent gametic and zygotic series, so that when a suspected case of coupling or repulsion comes to notice the nearest integral gametic series can at once be determined by inspection of the table, without making the calcu-

[1] No coupling.

[2] Not distinguishable from the case in which A and B are due to a single genetic factor.

lation anew. With the idea that these tables may possibly be useful to others, they are given herewith. In making use of such tables it is necessary only to reduce to the basis of a common total the observed F_2 zygotic series and any series of the table with which a comparison is desired. The total given in the table is in each case the lowest one which involves no fractions. If one uses the tables, such formulæ as Emerson's (II–IV) will not be found necessary in estimating the strength of the linkage. Moreover those formulæ are less useful than tables in dealing with the modified dihybrid ratio, 9:3:4, which happens to have been the first case that I encountered in my own work. The modified ratio as affected by linkage may be read directly from the table by combining classes aB and ab.

TABLE II

THE F_2 RATIO, 9:3:3:1, AS AFFECTED BY REPULSION (NEGATIVE LINKAGE), A AND B ENTERING THE F_1 ZYGOTE IN DIFFERENT GAMETES

Ratio, Cross-over to Non-cross-over Gametes	Proportion Cross-over Gametes	F_2 Zygotes				
		AB	Ab	aB	ab	Total
$1:x$	$\frac{1}{x+1}$	$2(x^2+2x)+3$	x^2+2x	x^2+2x	1	$(2x+2)^2$
1:1[3]	1/2	9	3	3	1	16
1:2	1/3	19	8	8	1	36
1:3	1/4	33	15	15	1	64
1:4	1/5	51	24	24	1	100
1:5	1/6	73	35	35	1	144
1:6	1/7	99	48	48	1	196
1:7	1/8	129	63	63	1	256
1:8	1/9	163	80	80	1	324
1:9	1/10	201	99	99	1	400
1:99	1/100	20,001	9,999	9,999	1	40,000
Limiting values[4]		2	1	1	0	4

[3] No repulsion.

[4] Not distinguishable from the case in which A and B are allelomorphs.

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BUSSEY INSTITUTION,
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